Genetic relationship between longevity and objectively or subjectively assessed performance traits in sheep using linear censored models

Mekkawy, W.; Roehe, R.; Lewis, R. M.; Davies, M. H.; Bunger, L.; Simm, G.; Haresign, W.

Published in:
Journal of Animal Science

DOI:
10.2527/jas.2008-1398

Publication date:
2009

Citation for published version (APA):
Mekkawy, W., Roehe, R., Lewis, R. M., Davies, M. H., Bunger, L., Simm, G., & Haresign, W. (2009). Genetic relationship between longevity and objectively or subjectively assessed performance traits in sheep using linear censored models. *Journal of Animal Science*, *87*(11), 3482-3489. https://doi.org/10.2527/jas.2008-1398

Genetic relationship between longevity and objectively or subjectively assessed performance traits in sheep using linear censored models

W. Mekkawy, R. Roehe, R. M. Lewis, M. H. Davies, L. Bünger, G. Simm and W. Haresign

J ANIM SCI 2009, 87:3482-3489.
doi: 10.2527/jas.2008-1398 originally published online July 31, 2009

Genetic relationship between longevity and objectively or subjectively assessed performance traits in sheep using linear censored models[1]

W. Mekkawy,*† R. Roehe,*[2] R. M. Lewis,‡ M. H. Davies,§ L. Bünger,* G. Simm,* and W. Haresign#

*Sustainable Livestock Systems Group, Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, United Kingdom; †Animal Production Department, Faculty of Agriculture, Ain Shams University, Hadaeq Shubra 11241 Cairo, Egypt; ‡Department of Animal and Poultry Sciences (0306), Virginia Polytechnic Institute and State University, Blacksburg 24061; §ADAS Rosemaund, Preston Wynne, Hereford HR1 3PG, United Kingdom; and #Institute of Biological Environmental and Rural Sciences, Llanbadarn Campus, Aberystwyth University, Ceredigion, SY23 3AL, United Kingdom

ABSTRACT: Genetic parameters of longevity in crossbred Mule ewes, and genetic relationships among longevity, growth, body composition, and subjectively assessed traits on Mule lambs and ewes have been estimated using Bayesian linear censored models. Additionally, the genetic associations between longevity and culling reasons were examined. Data comprised 1,797 observations of Mule ewes for longevity, culling reasons, growth, body composition, mouth scores, and type traits. Longevity was defined as the time (in years) from 2 yr of age (the age at first lambing of most ewes) to culling or death. Censored data (i.e., observations for which only the lower bound of the true longevity is known, such as when the animals are still alive) comprised 24% of all observations for longevity. Bivariate analyses were used to analyze the longevity of the ewe with each performance trait by fitting linear Bayesian models considering censored observations. Longevity was split into 3 different sub-traits: age at culling due to teeth/mouth conditions, age at culling due to udder conditions, and age at culling due to other culling reasons. These sub-traits and their aggregation into the overall trait of longevity were analyzed in a multiple-trait model. The heritability of longevity was moderate at 0.27, whereas heritabilities of the growth and body composition traits ranged from 0.11 for average of shoulder, loin, and gigot conformation to 0.36 for ewe BW at first premating. Mouth scores and type traits had heritabilities ranging from 0.13 for jaw position to 0.39 for fleece quality. All analyzed traits showed low genetic correlations with longevity, ranging from –0.20 for average conformation scores in live animals to 0.18 for tooth angle. Teeth/mouth conditions resulted in the greatest heritability (0.15) among the sub-traits based on the separate culling reasons. Genetic correlations between separate culling reasons were low to high (0.12 to 0.63 for teeth/mouth conditions with udder conditions and other culling reasons, respectively). Longevity may be preferred as a selection criterion because of (i) its moderate heritability compared with its component sub-traits based on specific culling reasons, and (ii) its moderate to high genetic correlation with these component sub-traits. The moderate heritability for longevity reflects the potential of this trait for genetic improvement, especially when longevity is based on clearly defined culling reasons.

Key words: Bayesian analysis, censored data, genetic parameter, longevity, sheep

J. Anim. Sci. 2009. 87:3482–3489
doi:10.2527/jas.2008-1398

INTRODUCTION

Longevity, or length of productive life of a ewe, is a trait of high economic importance because increased longevity decreases culling rates and female replacement costs. However, selection for longevity results in a longer generation interval.

Traits recorded in young animals are potential early predictors of longevity if genetically correlated. van Heelsum et al. (2006) showed moderate to high heritabilities for growth, body composition, mouth scores,

[1]We are grateful to the Department for Environment, Food and Rural Affairs (London, UK) and the Meat and Livestock Commission (Milton Keynes, UK) for funding, and to the Penglas Bluefaced Leicester Group Breeding Scheme members for the loan of rams. Thanks are also extended to the technical and support staff involved in the project. We are grateful to Ignacy Misztal (Department of Animal and Dairy Science, University of Georgia) for providing the genetic software.

[2]Corresponding author: Rainer.Roehe@sac.ac.uk

Received August 13, 2008.
Accepted July 22, 2009.

and other type traits in lambs. However, few genetic parameter estimates are available for longevity and its correlation with other traits in sheep, and those estimates are needed on predominant breed-types and crosses.

Ewes are culled for various reasons including udder condition, mouth and teeth loss, and other often disease-based causes. Longevity therefore is composed of several component traits, and their interrelationships are of considerable interest.

Different approaches are used for genetic evaluation of longevity including survival analysis (Ducrocq et al., 1988; Ducrocq, 1994) and linear models (Kersey DeNise et al., 1987; El-Saied et al., 2005). Survival analysis offers several advantages including use of censored and uncensored records (Vukasinovic et al., 1999; Caraviello et al., 2004). However, survival analyses are computationally demanding (Guo et al., 2001) and difficult to fit using multivariate models (Damgaard and Korsgaard, 2006a,b; Tarrés et al., 2006), with resulting parameters difficult to interpret. Linear model analyses overcome such limits and can be implemented considering censoring (Guo et al., 2001).

The aims of this study were to estimate the (crossbred) heritability of longevity in Mule ewes [crosses between Bluefaced Leicester (**BFL**) sires and hill breed ewes] and to examine the genetic relationships between longevity and traits measured in young animals, fitting a linear multiple-trait model with censoring. In addition, genetic associations between longevity and its component traits were examined.

MATERIALS AND METHODS

The Animal Experiment Committees at the Institute of Biological Environmental and Rural Sciences, the Scottish Agricultural College, and ADAS approved all procedures and protocols used in the experiment.

Animals

Over a 3-yr period (1998 to 2000), 1,500 hill ewes of 2 different breeds, Scottish Blackface and Hardy Speckled Face, were mated each year to 15 different BFL rams (n = 45 different BFL rams in total selected to represent the full range of growth and carcass traits within the breed) at 3 experimental farms in Wales (ADAS Pwllpeiran, IRS Tan-y-graig, and IRS Morfa Mawr in Wales, UK). The Mule ewe lambs produced were then distributed to 3 different evaluation sites in England, Scotland, and Wales, ensuring a balance of the progeny from the 45 sires used across these 3 Mule ewe evaluation sites. The Mules were first mated at approximately 18 mo of age to terminal sire rams (Charollais, Suffolk, and Texel in approximately equal proportions) in single sire mating groups.

All Mule ewe lambs were assessed for growth, body composition, mouth score, and type traits. Age at assessment ranged from 180 to 208 d (average 195 d), and the assessment took place each year around mid-October. In addition, the BW and BCS of Mule ewes before their first mating were recorded. Table 1 shows the description of performance traits measured on Mule ewe lambs at assessment days in October of each year and on Mule ewes at first premating, with indications of whether the trait was objectively or subjectively assessed. The data set consisted of 1,797 records of Mule ewes with growth, body composition, mouth score, and type traits. The pedigree file consisted of 2,196 animals, which included ancestry of the BFL rams that were used through their grandparents. Further detailed information on the design of the study and the characteristics of the data are provided by van Heelsum et al. (2006).

Longevity was recorded on these 1,797 Mule ewes and defined as the time (in years) from 2 yr of age (equivalent to the age at first possible lambing) to culling or death. The ewes were assessed every year between August and September for several health-related traits, their suitability to remain within the breeding flock, and for those ewes that had died, the reasons for death. Ewes remained within the breeding flock and were mated each year until they died or were culled for normal husbandry reasons. Reasons for culling were grouped into 3 categories: (i) udder condition, such as mastitis, (ii) teeth loss/mouth condition, but only if it precluded them from recovering adequate body condition between weaning and the onset of the next mating season, or (iii) for other (unspecified) conditions or death. The percentages of ewes that were culled or that died, according to the detailed reason and age of culling/death, are shown in Table 2. The opportunity existed for ewes to produce between 6 and 8 lamb crops, depending on their year of birth. Ewes that remained within the breeding flock after their sixth lambing or had gone missing (no death or culling record available) were treated as censored records. Censored data represented 24% of the entire observations for longevity (404 ewes that remained in the flock and 27 ewes that were missing). Data after the sixth lambing were not recorded.

Statistical Analyses

Growth, Body Composition, Mouth Scores, and Type Traits of Mule Ewe Lambs. In a previous study by van Heelsum et al. (2006), the growth, body composition, mouth scores, and type traits of the Mule ewe lambs were analyzed using REML. The same statistical model was fitted in the present study. The model included as fixed effects year-farm [9 levels; 3 farms and 3 yr (1998, 1999, or 2000)], birth-rearing type (4 classes), age of rearing dam (4 classes), and rearing classification (fostered or reared by dam). Age at assessment was included as a covariate in the model for growth, body composition, and type traits. In the pedigree, unknown parents were assigned to 3 different genetic groups (group 1 for Scottish Blackface, group 2

Table 1. Description of traits measured on Mule ewe lambs at assessment days in October, and Mule ewes before their first mating, including an indication of which traits were assessed subjectively

Trait group	Subjective[1]	Description
Growth/body composition		Assessed between 180 and 210 d of age of lambs
		BW at assessment in October, kg
		Ultrasonic muscle depth at third lumbar position, mm
		Ultrasonic fat depth at third lumbar position (average of 3 measurements)
	*	Average of shoulder, loin, and gigot conformation scores in live animals (scale 1 to 6)
Growth/body composition		Assessed before first mating at 18 mo of age of ewes
		BW at first premating, kg
	*	BCS at first premating; scale 1 (poor) to 5 (ideal)
Mouth scores[2]		Assessed between 180 and 210 d of age of lambs
	*	Jaw position; scale –5 (lower jaw 5 mm back from upper jaw) to 5 (lower jaw 5 mm in front of upper jaw)
	*	Tooth angle; scale –3 (45° forward) to 3 (45° back); ideal position is at right angle with lower jaw
	*	Tooth length; scale –2 (very short) to 2 (very long)
Overall type traits[3]		Assessed between 180 and 210 d of age of lambs
	*	Style or breed type; scale 1 (poor) to 10 (ideal); includes alertness, prowess, shape and position of head and ears, and length of neck and body
	*	Fleece quality and uniformity throughout the body; scale 1 (poor) to 10 (ideal)
	*	Structural soundness; scale 1 (poor) to 10 (ideal); indicates correctness of limbs (angle of pasterns, straightness of legs)

[1]Subjectively assessed traits are indicated with an asterisk; all other traits are measured objectively.
[2]Trait assessed by 1 experienced assessor.
[3]Trait assessed by a team of 3 highly experienced industry representatives.

for Hardy Speckled Face, and group 3 for BFL) using the method described by Westell et al. (1988). As random effects, the additive genetic effect of the animal, the maternal environmental effect of the litter, and the residual effect were fitted in the model. Some of the fixed effects were nonsignificant ($P > 0.05$) for some traits, and where this was the case they were excluded from the model: foster and dam age effects were excluded from the model for mouth score and type traits, and age at assessment and litter effect were excluded for mouth scores. Further information on the model fitted for each trait is provided by van Heelsum et al. (2006).

Growth and Body Composition of Mule Ewes. For BW and BCS at first premating, the fixed effects included in the model were year-farm of birth (9 levels), age of rearing dam (4 classes), and age of ewe at weighing as a covariate. The additive genetic effect of the animal, accounting for genetic groups, and residual effect were fitted as random effects.

Longevity and Performance Traits of Mule Ewes. A linear Bayesian model allowing for censoring

Table 2. Percentages of Mule ewes culled/died by reason and by age (percentage of total number in age group at beginning of the year)

	Age of ewe at culling/death, yr					
Reason for culling/death	2	3	4	5	6	7+
Total no. of ewes	1,797	1,614	1,397	1,167	886	568
Culling						
Teeth/mouth condition	0.2	0.4	3.4	10.9	22.1	18.3
Udder condition	4.1	4.6	5.8	6.9	5.2	3.5
Prolapse	0.7	0.6	0.6	1.2	0.9	0.5
Foot/leg problems	1.3	1.4	1.0	1.0	1.1	0.2
Other injury/abnormality	0.4	0.3	0.3	0.3	0.3	0.2
Poor body condition	0.3	0.2	0.4	1.0	4.0	4.2
Barren twice	0.0	1.5	0.4	0.4	0.8	0.7
Death						
Pregnancy-associated	0.0	0.2	0.3	0.2	0.3	0.0
Lambing associated	0.9	1.4	1.0	0.5	0.3	0.5
Internal sickness/disease	1.6	1.9	1.3	0.7	0.3	0.4
Injury	0.3	0.2	0.1	0.0	0.0	0.0
Unknown reason	0.3	0.4	1.0	0.7	0.3	0.4
Gone missing	0.1	0.3	0.9	0.3	0.3	0.0
Total	10.2	13.4	16.5	24.1	35.9	28.9

was used to analyze longevity. It included as fixed effects the year-farm of culling (21 levels), and as random effects the additive genetic effect of the animal, including genetic group assignments, and the residual effect. This same model was fitted for longevity in bivariate analyses when estimating the genetic co-variation for ewe longevity with each of the growth, body composition, mouth score, and type traits.

Longevity and Culling Reasons for Mule Ewes. In the present study, the ewes were mainly culled due to unsound teeth or mouths, or udder condition (Table 2). Culling reasons were therefore split into 3 sub-groups: (i) age at culling due to unsound teeth or mouth, (ii) age at culling due to udder condition, and (iii) age at culling due to other reasons. These traits, together with their genetic co-variation with overall longevity, were analyzed by fitting a multiple trait model that included the same fixed effects as described previously for longevity. Animals culled for 1 of these 3 culling reasons were treated as censored observations for the remaining culling reasons. This approach was initially known as competing risk analysis, where each nonculled ewe has an associated risk of culling for each culling reason (Southey et al., 2004). Zero residual covariances among culling reason traits were assumed as described by Arango et al. (2005).

Analytical Algorithm. Analyses were carried out using the GIBBSCF90 program based on the Markov Chain Monte Carlo approach. The GIBBSCF90 program is a modification of GIBBSF90 allowing use of a linear model that accounts for censored data (Misztal et al., 2002). Flat priors for the systematic and random effects were assumed. The marginal posterior distributions of the parameters of interest were obtained using Gibbs sampling. For each analysis a single chain of 100,000-cycles length was generated. A burn-in period of 10,000 iterations was used, as well as a lag between cycles of 10 to reduce the autocorrelations among samples. A total of 9,000 samples were kept for computation of the posterior means, SD, and 95% highest posterior density regions (**$HPD_{95\%}$**) of heritabilities, and genetic and phenotypic correlations of longevity with performance traits. Convergence was checked using the algorithms of Raftery and Lewis (1992).

RESULTS AND DISCUSSION

The percentages of ewes that were culled or dead, categorized by age and reason for culling or death, are presented in Table 2. Younger ewes were most commonly culled for udder condition (mastitis). As expected, the number of culls for teeth/mouth condition was small for 2-, 3-, and 4-yr-old ewes, but then increased substantially for older age groups. In the 3 oldest age categories, substantially more ewes were culled for teeth/mouth condition than for udder condition. The most frequent cause of death was internal sickness or disease, which included severe mastitis, pneumonia, and listeriosis. The second most frequent cause of death was lambing-associated, which included septicemia and prolapse. Losses due to death were largely independent of ewe age. The total percentage of ewe losses (of those remaining in the flock each year) due to culling and death combined remained relatively constant up to 4 yr of age, but then increased due to the age-related increase in culling for teeth and mouth condition.

Heritabilities of Longevity, Growth, Body Composition, Mouth Score, and Type Traits

Estimates of posterior means and $HPD_{95\%}$ regions of heritabilities for longevity, growth, and type traits are presented in Table 3. The posterior mean of the heritability for longevity was 0.27 with $HPD_{95\%}$ ranging from 0.22 to 0.33. There are few reports in the literature of genetic parameters for ewe longevity in sheep, and those available generally suggest the trait is lowly heritable. For Churra ewes, estimates of the heritability for longevity ranged from 0.02 to 0.06 (El-Saied et al., 2005). Brash et al. (1994) and Conington et al. (2001) also reported low heritabilities for ewe longevity at 0.06 and 0.08, respectively, in Australian Dorset and Scottish Blackface sheep.

The moderate heritability estimate for ewe longevity in the current study may be due to several factors. First, the animals were all kept on experimental farms where the husbandry and other environmental effects were carefully controlled. Second, tightly defined reasons for culling were applied across all 3 farms. Third, because the estimate was derived from information on crossbred Mule ewes, rather than from a purebred population, it may be inflated by nonadditive variation, which is the basis for heterosis effects on performance traits. This was inescapable because the aim of the experiment was to improve the longevity of crossbred Mule ewes, and longevity data were only available on such crossbred ewes. Currently, there are few performance-recorded BFL flocks in the United Kingdom, and thus relevant purebred data are unavailable. Furthermore, although heritability estimates may be inflated in crossbred populations, they are still indicative of the opportunity for achieving genetic change for traits, such as longevity, central to a specific crossbreeding system.

Linear models considering censoring have not been used in sheep before, but they have been used in pigs. Guo et al. (2001) estimated the heritability of the length of productive life in Landrace sows at 0.25 using a Bayesian linear model with censoring. This estimate increased to 0.34 when censored records were excluded from the data. Also, Arango et al. (2005) reported heritabilities of the disposal codes of Large White sows ranging from 0.13 to 0.18 using a linear model considering censoring.

The heritabilities of mouth score traits in Mule ewe lambs were low to moderate, with the least value for jaw position (0.13) and greatest value for tooth length (0.31). For growth and body composition traits, the heritability estimates in Mule ewe lambs ranged from

Table 3. Posterior means of the heritabilities of ewe longevity, growth/body composition, mouth score, and overall type traits

Trait	Heritability[1]
Longevity of ewes	0.27 (0.22 to 0.33)
Growth/body composition of Mule ewe lambs	
BW at assessment in October	0.14 (0.04 to 0.25)
Ultrasonic muscle depth at third lumbar position	0.15 (0.06 to 0.26)
Ultrasonic fat depth at third lumbar position	0.23 (0.11 to 0.37)
Average of shoulder, loin, and gigot conformation scores in live animals	0.11 (0.02 to 0.19)
Growth/body composition traits of Mule ewes	
BW at first premating, 18 mo of age	0.36 (0.17 to 0.56)
BCS at first premating	0.24 (0.12 to 0.37)
Ultrasonic muscle depth at first premating	0.22 (0.10 to 0.36)
Ultrasonic fat depth at first premating	0.32 (0.17 to 0.47)
Mouth scores of Mule ewe lambs	
Jaw position	0.13 (0.04 to 0.24)
Tooth angle	0.20 (0.09 to 0.32)
Tooth length	0.31 (0.16 to 0.50)
Overall type traits of Mule ewe lambs	
Style or breed type	0.23 (0.09 to 0.39)
Fleece quality and uniformity throughout the body	0.39 (0.14 to 0.64)
Structural soundness	0.24 (0.09 to 0.41)

[1]The 95% highest posterior density regions intervals are in parentheses.

0.11 for average of shoulder, loin, and gigot (leg) conformation to 0.23 for ultrasonic fat depth. These estimates were less than those of corresponding traits of Mule ewes at first premating, which ranged from 0.22 for ultrasonic muscle depth to 0.36 for ewe BW.

The estimated heritabilities of performance traits were similar to those obtained by van Heelsum et al. (2006). This is not surprising because similar data and the same effects were fitted in the statistical model. The heritabilities for BW at assessment in October (0.23), and style or breed type (0.36), reported by van Heelsum et al. (2006) were slightly greater than those estimated in the current study. The differences may be due to reduction in size of the data set; in the present analyses only records of animals reaching 2 yr of age were considered. In addition, the heritabilities reported by van Heelsum et al. (2006) were averages from bivariate analyses undertaken to obtain correlations among all pairs of traits. In the present analysis, every trait was only assessed once alongside longevity.

Genetic Correlations Between Longevity and Growth, Body Composition, Mouth Score, or Type Traits

All growth, body composition, mouth scores, and type traits showed low genetic correlations with longevity, ranging from –0.20 for average conformation scores in live animals to 0.18 for tooth angle as presented (Table 4). However, none of these correlations was substantially different from zero, indicating that they are not useful as early genetic predictors for ewe longevity. The phenotypic correlations between longevity and growth, body composition, mouth score, or type traits were even less than the corresponding genetic correlations (Table 5).

It is still possible that these performance and type traits, measured at an early stage of the life of the ewe lamb, may be correlated with survival from birth to first lambing. That time frame would define a different trait than ewe longevity as used in the present study, which was the time from first lambing to culling. In dairy cattle, Forabosco et al. (2004) pointed out that survival from birth to first calving is a different trait than longevity from first calving to culling because of biological differences and management policies of farmers. They recommended treating these survival characteristics as different traits, considering their low genetic correlation.

Theoretically, a joint survival analysis of longevity with all performance traits would be the most appropriate approach for parameter estimation. The model complexity and high computational requirements, especially for large size data sets, are the main limiting factors for adopting that strategy. Therefore, studies of the genetic relationships between longevity and growth, body composition, or type traits are rare in the literature. Very often the relationships of longevity with performance traits are only estimated by including the latter traits as fixed effects in the survival analysis to identify their importance on longevity (Buenger et al., 2001; Caraviello et al., 2004; Forabosco et al., 2004; Sewalem et al., 2005).

To overcome the computational difficulties associated with survival analyses, Tarrés et al. (2006) suggested a 2-step approach to approximate the genetic correlations between longevity and linear performance traits. Vollema and Groen (1997) indicated that the main difference between a linear model and a survival analysis for longevity arises from ignoring censored data. However, in the present study, censoring was accounted for using a Bayesian approach. Moreover, Guo et al. (2001)

Table 4. Posterior means of the genetic correlations of ewe longevity with growth/body composition, mouth scores, and overall type traits

Trait	Genetic correlation with ewe longevity[1]
Growth/body composition of Mule ewe lambs	
BW at assessment in October	−0.02 (−0.42 to 0.36)
Ultrasonic muscle depth at third lumbar position	−0.09 (−0.50 to 0.25)
Ultrasonic fat depth at third lumbar position	−0.07 (−0.38 to 0.27)
Average of shoulder, loin, and gigot conformation scores in live animals	−0.20 (−0.73 to 0.27)
Growth/body composition of Mule ewes	
BW at first premating, 18 mo of age	0.10 (−0.20 to 0.40)
BCS at first premating	−0.07 (−0.44 to 0.29)
Ultrasonic muscle depth at first premating	−0.19 (−0.54 to 0.16)
Ultrasonic fat depth at first premating	0.01 (−0.28 to 0.30)
Mouth scores of Mule ewe lambs	
Jaw position	0.06 (−0.44 to 0.53)
Tooth angle	0.18 (−0.15 to 0.53)
Tooth length	0.10 (−0.21 to 0.40)
Overall type traits of Mule ewe lambs	
Style or breed type	−0.05 (−0.41 to 0.29)
Fleece quality and uniformity throughout the body	0.06 (−0.19 to 0.32)
Structural soundness	−0.06 (−0.41 to 0.33)

[1]The 95% highest posterior density regions intervals are in parentheses.

emphasized that ignoring the censored data in the genetic evaluation may lead to distorted inferences, which could modify the outcome of the selection decision.

Longevity and Culling Reasons

Posterior means of heritabilities, and genetic and residual correlations, derived from bivariate analyses among overall longevity and its sub-traits (culling reasons), are presented in Table 6. Estimated heritabilities ranged from 0.06 for age at culling due to inferior udder condition to 0.26 for longevity considering all culling reasons. Age at culling due to inferior teeth/mouth condition resulted in the greatest sub-trait heritability (0.15) among all specific culling reasons.

Genetic correlations between the individual sub-traits (culling reasons) were low to high (0.12 to 0.63). In particular, the low nonsignificant genetic correlation between culling due to teeth and mouth condition and udder condition (0.12) suggests that these traits are influenced by different genetic effects. While culling due to teeth and mouth condition was highly genetically correlated (0.63) with culling due to other reasons, culling due to udder condition showed a nonsignificant low genetic correlation (0.21) with culling due to other reasons. However, all genetic correlations among culling

Table 5. Posterior means of the phenotypic correlations of ewe longevity with growth/body composition, mouth scores, and overall type traits

Trait	Phenotypic correlation with ewe longevity[1]
Growth/body composition of Mule ewe lambs	
BW at assessment in October	0.00 (−0.06 to 0.06)
Ultrasonic muscle depth at third lumbar position	0.01 (−0.06 to 0.07)
Ultrasonic fat depth at third lumbar position	0.00 (−0.06 to 0.06)
Average of shoulder, loin, and gigot conformation scores in live animals	0.00 (−0.07 to 0.05)
Growth/body composition of Mule ewes	
BW at first premating, 18 mo of age	0.03 (−0.04 to 0.10)
BCS at first premating	0.01 (−0.06 to 0.07)
Ultrasonic muscle depth at first premating	−0.01 (−0.08 to 0.05)
Ultrasonic fat depth at first premating	0.03 (−0.04 to 0.09)
Mouth scores of Mule ewe lambs	
Jaw position	0.06 (−0.01 to 0.12)
Tooth angle	0.02 (−0.05 to 0.08)
Tooth length	0.02 (−0.05 to 0.09)
Overall type traits of Mule ewe lambs	
Style or breed type	0.00 (−0.07 to 0.07)
Fleece quality and uniformity throughout the body	0.01 (−0.05 to 0.08)
Structural soundness	−0.02 (−0.09 to 0.05)

[1]The 95% highest posterior density regions intervals are in parentheses.

Table 6. Posterior means, 95% highest posterior density regions ($HPD_{95\%}$) of residual correlations (above diagonal), heritabilities (on diagonal, marked with *), and genetic correlations (below diagonal) for age due to culling reasons and ewe longevity[1]

Trait[2]	Longevity	TMC	UC	OR
Longevity	0.26 (0.22 to 0.30)*	0.40 (0.34 to 0.45)	0.18 (0.13 to 0.24)	0.26 (0.21 to 0.32)
TMC	0.87 (0.77 to 0.96)	0.15 (0.11 to 0.19)*	—[3]	—
UC	0.51 (0.29 to 0.69)	0.12 (−0.21 to 0.43)	0.06 (0.03 to 0.10)*	—
OR	0.79 (0.62 to 0.95)	0.63 (0.32 to 0.91)	0.21 (−0.19 to 0.58)	0.08 (0.05 to 0.12)*

[1]$HPD_{95\%}$ intervals are in parentheses.

[2]TMC = age at culling due to teeth/mouth condition; UC = age at culling due to udder condition; and OR = age at culling due to other culling reasons; ewe longevity is the composite of all described culling reasons.

[3]Residual correlations between separate culling reasons were assumed to be 0 because observations of animals culled for a specific reason were treated as censored observations in the other culling reason.

reasons were positive, so that no reduction in genetic response due to antagonistic genetic associations is expected.

The genetic correlations between overall ewe longevity and its component sub-traits were all moderate to high (0.51 to 0.87). This indicates that selection for overall longevity will substantially improve the component traits associated with teeth and mouth, udder, and other conditions. The residual correlations between overall longevity and its sub-traits (culling reasons) ranged from 0.18 to 0.40. This suggests that genetic associations between longevity and its component sub-traits are larger than those due to environmental effects. The residual correlations between separate culling reasons were assumed to be zero because observations of animals culled for 1 specific reason were treated as censored observations in the other culling reason.

Longevity is typical of a class of traits that involve a time to some event or end-point and that are not normal in their distribution. For such traits, survival analysis is preferred as an appropriate method for analysis. Nevertheless, multivariate models are not easy to fit with survival analysis. The use of linear models with censoring provides an efficient implementation of multiple-trait analysis of longevity with other performance traits.

Genetic correlations between ewe longevity and growth, body composition, mouth scores, or type traits were low and not significantly different from 0, which indicates that ewe longevity is not influenced by performance traits measured early in life. Overall, longevity showed a moderate heritability, which was substantially greater than the estimates for its component sub-traits. The substantial genetic determination of longevity reflects the potential to make genetic progress by selection for longevity without affecting those early lamb and ewe performance traits included in the present study. Consequently, the composite trait of ewe longevity may be the preferred selection criterion because longevity combined information from all of its various sub-traits (culling reasons), showed the greatest heritability of all traits associated with culling, and was sufficiently highly correlated with each separate culling reason. The fact that longevity was not genetically correlated with any of the performance and type traits measured in young animals means that it will need to be directly measured and included in any selection program in which its improvement is deemed important.

LITERATURE CITED

Arango, J., I. Misztal, S. Tsuruta, M. Culbertson, and W. Herring. 2005. Study of codes of disposal at different parities of Large White sows using a linear censored model. J. Anim. Sci. 83:2052–2057.

Brash, L. D., N. M. Fogarty, and A. R. Gilmour. 1994. Reproductive performance and genetic parameters for Australian Dorset sheep. Aust. J. Agric. Res. 45:459–468.

Buenger, A., V. Ducrocq, and H. H. Swalve. 2001. Analysis of survival in dairy cows with supplementary data on type scores and housing systems from a region of Northwest Germany. J. Dairy Sci. 84:1531–1541.

Caraviello, D. Z., K. A. Weigel, and D. Gianola. 2004. Comparison between a Weibull proportional hazards model and a linear model for predicting the genetic merit of US Jersey sires for daughter longevity. J. Dairy Sci. 87:1469–1476.

Conington, J., S. C. Bishop, A. Waterhouse, and G. Simm. 2001. Multi-trait selection indexes for sustainable U.K. hill sheep production. Anim. Sci. 73:413–423.

Damgaard, L. H., and I. R. Korsgaard. 2006a. A bivariate quantitative genetic model for a linear Gaussian and a survival trait. Genet. Sel. Evol. 38:45–64.

Damgaard, L. H., and I. R. Korsgaard. 2006b. A bivariate quantitative genetic model for a threshold trait and a survival trait. Genet. Sel. Evol. 38:565–581.

Ducrocq, V. P. 1994. Statistical analysis of length of productive life for dairy cows of the Normande breed. J. Dairy Sci. 77:855–866.

Ducrocq, V., R. L. Quaas, E. J. Pollak, and G. Casella. 1988. Length of productive life of dairy cows. 2. Variance component estimation and sire evaluation. J. Dairy Sci. 71:3071–3079.

El-Saied, U. M., L. F. De La Fuente, J. A. Carriedo, and F. San Primitivo. 2005. Genetic and phenotypic parameter estimates of total and partial lifetime traits for dairy ewes. J. Dairy Sci. 88:3265–3272.

Forabosco, F., A. F. Groen, R. Bozzi, J. A. M. Van Arendonk, F. Filippini, P. Boettcher, and P. Bijma. 2004. Phenotypic relationships between longevity, type traits, and production in Chianina beef cattle. J. Anim. Sci. 82:1572–1580.

Guo, S.-F., D. Gianola, R. Rekaya, and T. Short. 2001. Bayesian analysis of lifetime performance and prolificacy in Landrace sows using a linear mixed model with censoring. Livest. Prod. Sci. 72:243–252.

Kersey DeNise, R. S., D. E. Ray, A. M. Lane, V. L. Rundle, and M. Torabi. 1987. Relationships among udder shape, udder capacity, cow longevity and calf weights. J. Anim. Sci. 65:366–372.

Misztal, I., S. Tsuruta, T. Strabel, B. Auvray, T. Druet, and D. H. Lee. 2002. BLUF90 and related programs (BGF90). Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France. CD-ROM. Communication No. 28–07.

Raftery, A. E., and S. M. Lewis. 1992. How many iterations in the Gibbs sampler? Pages 763–774 in Bayesian Statistics IV. J. M. Bernardo, J. O. Berger, A. P. Dawid, and A. F. M. Smith, ed. Oxford Univ. Press, Oxford, UK.

Sewalem, A., G. J. Kistemaker, V. Ducrocq, and B. J. Van Doormaal. 2005. Genetic analysis of herd life in Canadian dairy cattle on a lactation basis using a Weibull proportional hazards model. J. Dairy Sci. 88:368–375.

Southey, B., R. Rodriguez-Zas, and K. A. Leymaster. 2004. Competing risks analysis of lamb mortality in a terminal sire composite population. J. Anim. Sci. 82:2892–2899.

Tarrés, J., J. Piedrafita, and D. Vincent. 2006. Validation of an approximate approach to compute genetic correlations between longevity and linear traits. Genet. Sel. Evol. 38:65–83.

van Heelsum, A. M., R. M. Lewis, M. H. Davies, and W. Haresign. 2006. Genetic relationships among objectively and subjectively assessed traits measured on crossbred (Mule) lambs. Anim. Sci. 82:141–149.

Vollema, A. R., and A. F. Groen. 1997. Genetic correlations between longevity and conformation traits in an upgrading dairy cattle population. J. Dairy Sci. 80:3006–3014.

Vukasinovic, N., J. Moll, and N. Künzi. 1999. Genetic evaluation for length of productive life with censored records. J. Dairy Sci. 82:2178–2185.

Westell, R. A., R. L. Quass, and L. D. Van Vleck. 1988. Genetic groups in an animal model. J. Dairy Sci. 71:1310–1318.